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THE EXTERNAL DEVELOPMENT OF THE BANDED DOGFISH OR POFADDERHAAI HAPLOBLEPHARUS EDWARDSII (M. & H.)

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INTRODUCTION

This oviparous species of dogfish, previously known as *Scylliorhinus edwardsii* (Cuv.), is endemic to South African waters and has been recorded from Saldanha Bay, Table Bay, False Bay and the Agulhas Bank. The largest one on record measured 520 mm. This dogfish is fairly plentiful and specimens are on exhibition in the Sea Point Aquarium.

On November 5, 1942, a female was observed to lay two egg cases in one of the tanks of the Aquarium. One case was immediately removed and dissected to expose the egg, whilst the other was left in the tank as a control in the determination of the duration of incubation.

The egg was completely removed from the egg case and placed under observation in running sea water.

THE FEMALE REPRODUCTIVE ORGANS

The only external sexual characters in the female are the pair of cloacal papillae (Plate I, c.p.), one situated on either side of the median line immediately posterior to the cloacal aperture. The papillae themselves are perforate, and the abdominal pore situated in the center of each papilla connects direct with the coelom. The actual function of these abdominal pores is not known and it is obvious that, in view of the highly specialized structure of the female genital system, they have lost the function of acting as apertures through which the ova leave the body.

A dissection (Plate I) revealed the fact that there was only a single median ovary (ov.) present which contained ova in various stages of development. The ovary is situated in the middle portion of the coelom and is relatively large. The paired oviducts are highly specialized both in structure and function. The oviducts meet medially in the anterior part of the coelom (f.t.o.). Each oviduct may be divided into four distinct portions as follows:

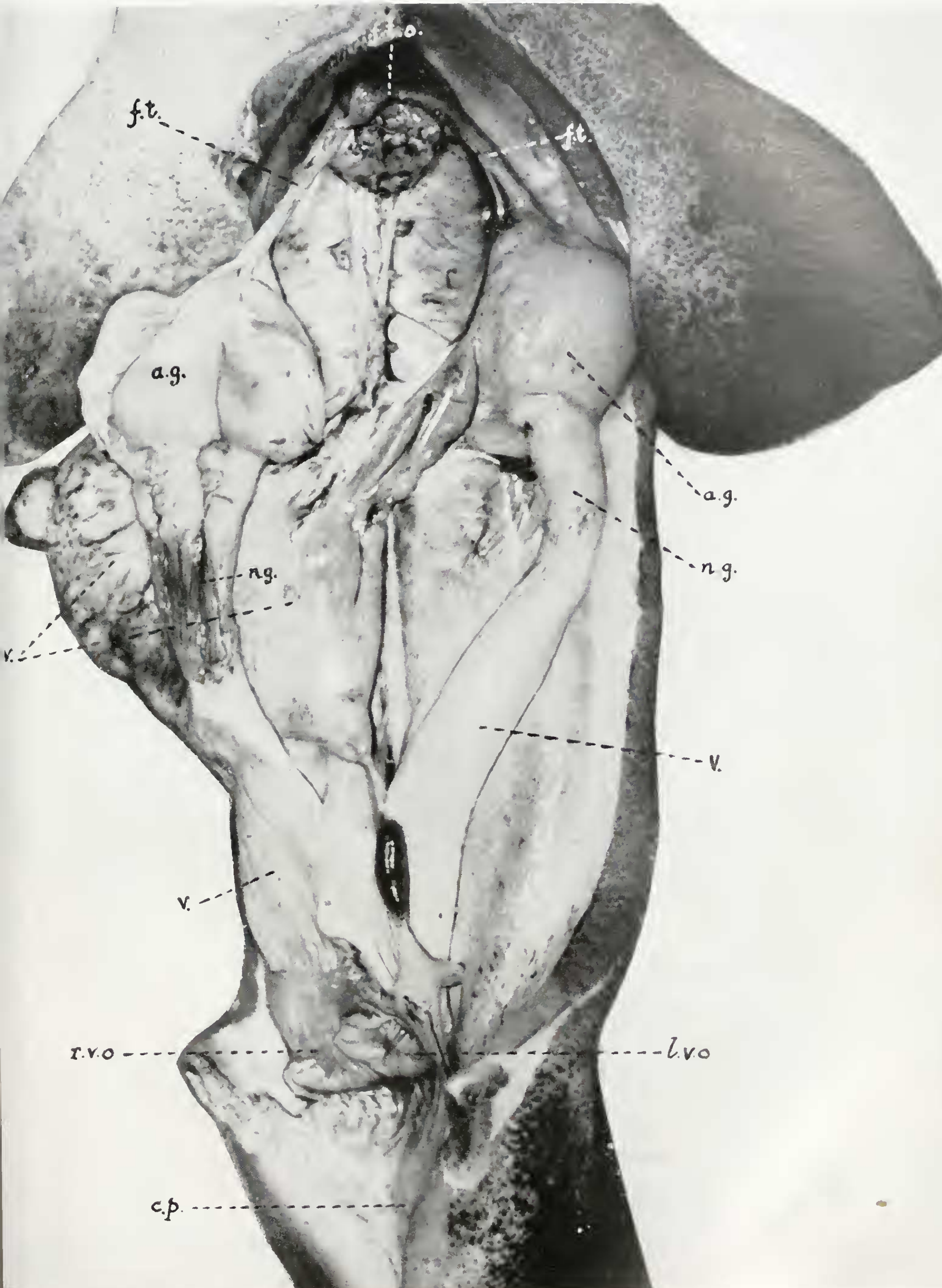
(1) The fallopian tube (Plates I and II, f.t.) is extremely narrow and thin-walled and is about a quarter of the length of the whole oviduct. Its internal surface is slightly convoluted longitudinally. This portion is followed by (2) the albumen gland (a.g.) which is about one-eighth of the total length of the oviduct and is very thick-walled and muscular. This gland secretes the albumen which sur-

rounds the ovum, hence its internal surface is richly supplied with glands for this purpose. A transverse section of the albumen gland (Plate II, Fig. 3, l.a.g.) shows that the lumen is extremely narrow, the walls of the gland being completely apposed. Smith (1942, p. 703) in describing Bashford Dean's figure of the reproductive organs of an adult female *Heterodontus japonicus* states—"This drawing (my Text-figure 35) is not labelled, nor is it described in Dean's notes, and in the absence of the dissection some features are obscure. In the mid-line near the top of the figure, one readily notes the common abdominal opening of the oviducts. On the extreme right side of the figure the oviduct with its three divisions—oviduct proper, shell gland, and uterine portion—are easily identified." The part of the oviduct designated "shell gland" in the above quotation is very similar in external appearance to that of the present species, but as previously stated, this swollen portion functions as the albumen gland in the present species. There are no indications of a laminated structure in this gland as described by Gudger (1940, p. 550) for the nidamental gland of Chlamydoselachus. Immediately following the albumen gland is (3) the nidamental gland (n.g.) which is also about one-eighth of the total length of the oviduct and secretes the shell around the ovum. The interior surface of the nidamental gland is extremely well convoluted and is of a dark yellowish color. Widakowich (1907, p. 527) states—"Das Nidamentalorgan von Acanthias besteht aus einem cranial gelegenen Teile, der, wenn man nach Analogie mit Scyllium schliessen darf, Eiweiss erzeugt, aus einem mittleren, der, wie sich zeigen lässt, die Schale liefert, und aus einem untersten, wohl Schleim produzierenden Abschnitte." As the functions of the various parts of the oviduct of the present species, however, are distinctly diverse, it appears to be better to look upon each part as an independently functioning entity and parts two and three as here described may be looked upon as analogous to the cranial portion, and the central and caudal portions of the nidamental gland, respectively, as described by Widakowich. The last part (4) of the oviduct is the vagina (v.), occupying about one-half of the total length. This portion of the oviduct is designated the vagina in analogy to the use of this term in mammals in view of the fact that the intromittent organs (claspers) of the male are inserted through the vaginal orifices during copulation.

Each oviduct opens separately by a vaginal orifice (Plate II, l.v.o. and r.v.o.) into the cloaca. The vagina is well convoluted longitudinally to permit of distension both during copulation and during ovulation. In certain of the females dissected, parts of the mermaid's purse were present in the upper half of the vagina where it leaves the nidamental gland. These parts consisted principally of the anterior and posterior parts of the mermaid's purse complete with the tendrils (see Plate IV, Fig. 6).

Plate I

Dissection showing the female reproductive organs of *Haploblepharus edwardssi* (M. & H.). a.g., albumen gland. c.p., cloacal papilla. e.g., external gill-filaments. f.t., fallopian tube. f.t.o., coelomic orifice of same. h., hooks of clasper. h′., hooks normally covered by rhipidion. hy., hypopyle. l.a.g., lumen of albumen gland. l.v.o., left vaginal orifice. n.g., nidamental gland. ov., ovary. r., rhipidion. r.v.o., right vaginal orifice (opened). u., umbilicus with remains of cord. u.c., umbilical cord. v., vagina. v.b.v., vitelline blood vessel. y.s., yolk sac.


o.
f.t.
f.t.
a.g.
a.g.
n.g.
n.g.
v.
V.
v.
r.v.o
l.v.o
c.p.

The Male Reproductive Organs

The morphology of the male reproductive system follows the general plan of all Elasmobranchs. The testes are paired and occupy the anterior half of the coelom. From the anterior end of each testis the vasa efferentia lead to the epididymus which is much coiled. The epididymus eventually widens out into the vas deferens which expands and joins its fellow in the median line posteriorly, opening into the cloaca by a single pore.

The secondary sexual characters of this species are very distinct and it is necessary to describe them in more detail. As in all male Elasmobranchs, the basal element of each pelvic fin (*basipterygium*) is prolonged to form a stout, backwardly-directed rod which is sharply demarcated from the remainder of the fin and specially modified to form an intromittent organ commonly known as the clasper or myxopterygium. In this species the clasper is a very highly differentiated organ which differs in many respects from that found in other Elasmobranchs. In transverse section the clasper is almost completely round in its proximal half, the internal cartilagenous skeleton forming a tube which is almost completely filled with a thick muscular substance through the center of which passes a duct. In the distal part the skeleton only occupies the ventral portion of the clasper, being continued right to the tip. The latero-dorsal wings of this portion of the clasper are formed of thickened skin, the outer wing being folded over the curved inner wing so as to form a canal which is a continuation of the duct in the proximal portion previously mentioned. This canal opens on the dorsal side of the posterior end of the clasper in the form of a hypopyle (Plate III, Fig. 4, hy.). Schmidt (1930) first noted the existence of hooks in the clasper of *Halaelurus torazama* which is a genus closely related to the present one and he noted that these hooks were approximately 100 in number. The clasper of the present species also shows approximately 100 hooks on the outer lateral wall of the clasper (h. and Fig. 5).

Schmidt states—"Considering now what purpose this arrangement can serve, one comes to the conviction that the hooks can be used only for fastening the clasper on the wall of the vaginal part of the oviduct of the female during the copulation. Probably, when the clasper is introduced, the borders of its gutter are turned out and all the hundred hooks of the row are imbedded in the oviducal wall, holding the clasper as anchors. If the other clasper is introduced simultaneously in the other oviduct, the male is held by 200 little anchors. This arrangement may be necessary, as the female of this shark is larger than the male, which is perhaps carried about by the female during a copulation that may continue for a very long time.

"This arrangement of the organs of copulation of the male seems to be unique not only among the fishes, but perhaps in the whole animal kingdom," but he makes no mention of the other series of hooks (h'.) which lie on the inner lateral wall of the clasper and which are covered by a rhipidion (r.), whose function is to spray the spermatozoa in all directions in a radiating manner, under the pressure exerted

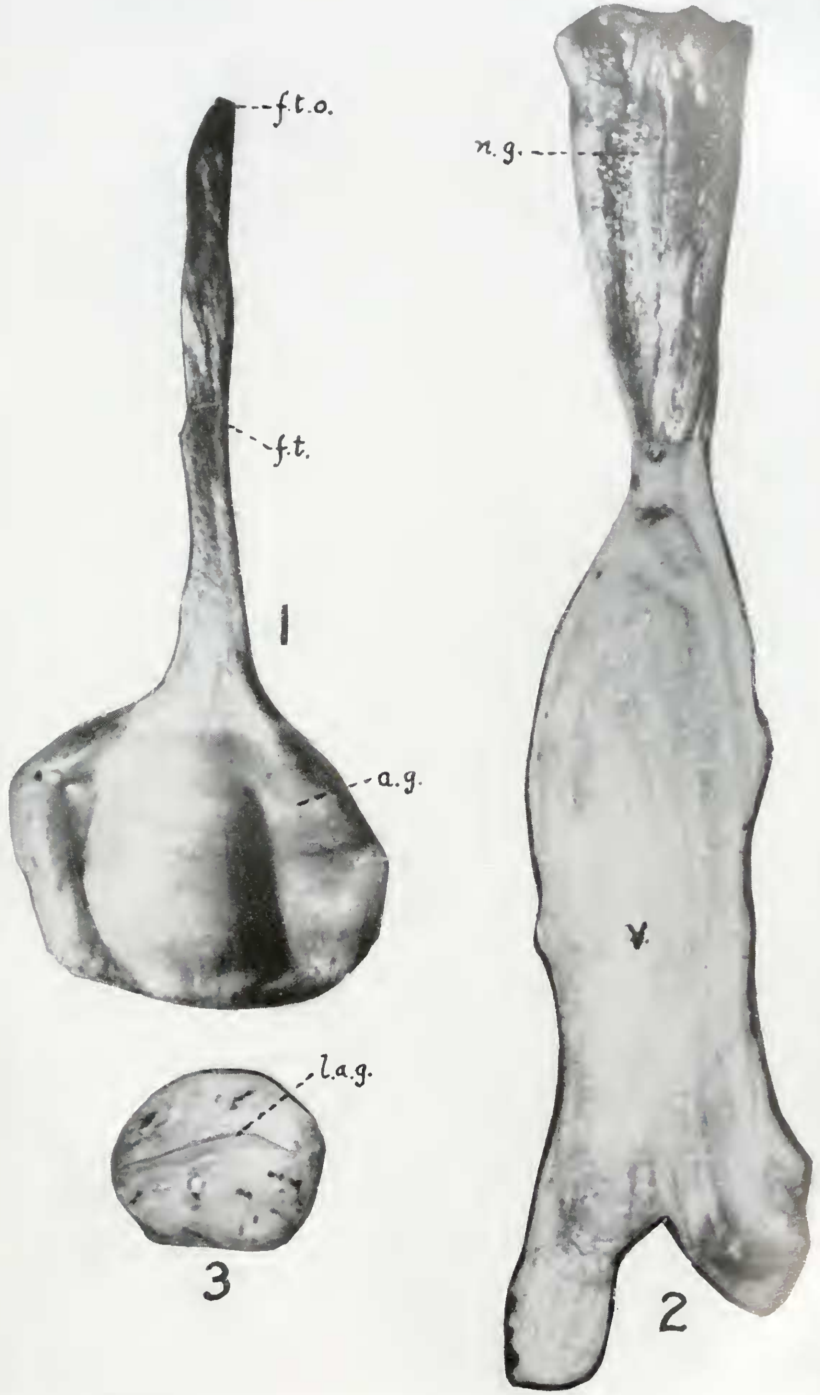
Plate II

The left oviduct opened medially to show the internal structure.

Figure 1. Longitudinal section through the fallopian tube and the albumen gland.

Figure 2. Longitudinal section through the nidamental gland and the vagina.

Figure 3. Sagittal section through the albumen gland.


f.t.o.
n.g.
f.t.
1
a.g.
v.
l.a.g.
3
2

by the water forcibly ejected by the siphon. The reason for this is obvious since fertilization takes place in the fallopian tubes and the spermatozoa, although motile, have to traverse the complete length of the vagina, nidamental gland, and the albumen gland to reach the ova in the anterior end of the fallopian tubes.

Leigh-Sharpe (1920) in describing the secondary sexual characters of *Scyllium catulus* mentions the presence of a siphon on the ventral surface of each pelvic fin. The present species also has such a siphon developed in the same position, although it is probably more analogous to the clasper gland mentioned by Leigh-Sharpe (op. cit., p. 260) than to the siphon. The whole of the clasper except the distal end is covered with dermal denticles. A deep dissection of the clasper showed that it is in no way innervated.

Development

In order to study the external development of this species a mermaid's purse was opened, the ovum removed from the purse and placed in a dish of running sea water. The albumen was completely removed so as to enable one to observe the development of the embryo.

The egg case or mermaid's purse (Plate IV, Fig. 6) is more or less typical of those formed by oviparous dogfishes. The anterior end is broad and almost as wide as the main body and has a straight edge where the two halves have partially coalesced. From each lateral end a long coiled filamentous process, which gradually becomes thinner towards the distal end, arises. Near the base of each of these tendrils the purse has a longitudinal slit-like aperture (s.) which leads to the interior. These apertures only appear on one surface of the egg case. Posteriorly the egg case tapers until it is little more than half as wide as the anterior end. At the lateral extremities of this sharper end two processes arise which are the bases of the tendrils. These posterior tendrils are much longer and thicker than the anterior ones at their points of origin, but, like the latter, they also become thinner towards their distal ends. It is this pointed end of the purse which first appears through the vaginal orifice when the egg case is laid. The function of the tendrils is to anchor the egg case securely to rocks or seaweed to prevent its being buffeted about by the waves. The egg case itself is formed from keratin secreted by the nidamental gland. Widakowich (1906) stated that the mermaid's purse of *Scyllium canicula* is formed by a large number of separate elements ("Platten") which later, on exposure to sea water, adhere closely to form a complete shell (see also Hobson (1930, p. 580)), but in *Haploblepharus edwardsii* there is no evidence of such a formation of the egg case which is here laid down completely in two halves, the dorsal and ventral parts, the edges of which coalesce.

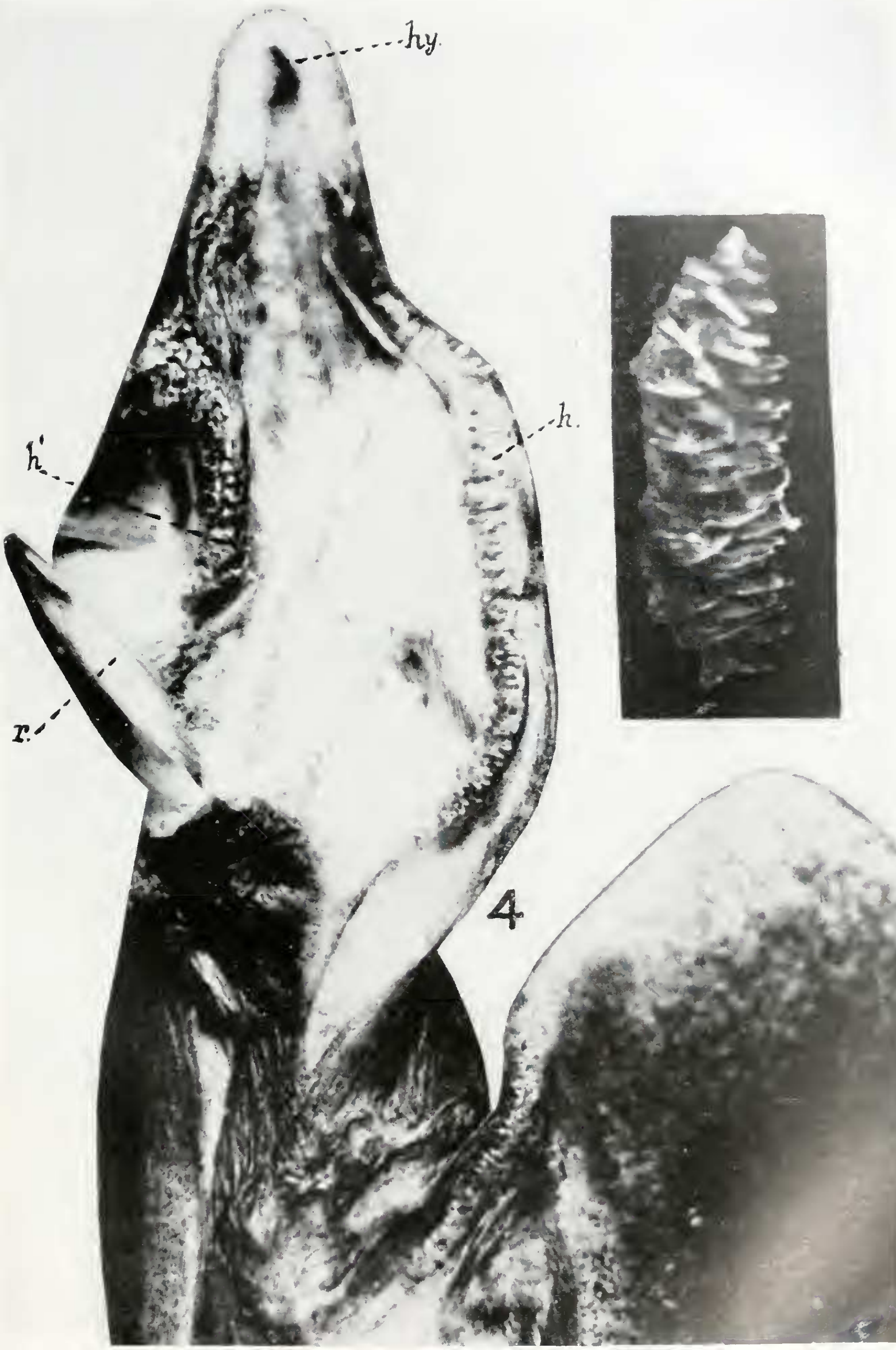
A dissection of the mermaid's purse shows that it is a structure formed of two portions which may be designated the dorsal and ventral halves, each half being hollow, the edges being apposed and completely fused along their whole length except at the blunt anterior end where the apposition is purely temporary. It is

PLATE III

FIGURE 4. Dorsal view of the left clasper with lateral wings of distal portion distended to show internal structure. × 4.

FIGURE 5. A series of 40 hooks removed from the clasper. × 10.

Plate III



through this anterior end that the fish eventually escapes, hence the lack of fusion of these edges. The swollen central portion occupying about two-thirds of the internal space of the egg case, is filled by the relatively enormous yolk. Surrounding the yolk and occupying the remaining space of the egg case is the thick viscid transparent albumen. From the fact that during the artificial rearing of the embryo away from the egg case all the albumen was removed from the yolk, it is obvious that this albumen plays no part in the development or nourishment of the embryo at any stage, and purely serves the purpose of a protective cover around the embryo during its development. Its function could be regarded more or less as that of a shock absorber analogous to the function of the amniotic fluid in higher vertebrates.

The egg itself is between 30 and 35 mm. in diameter and is typical of the majority of Selachian eggs in regard to the distribution of yolk, being telolecithal. On one surface of the egg, which may be looked upon as the dorsal aspect, lies the germinal disc which is slightly lighter in color than the rest of the egg, has a diameter of 1.2 mm., and contains practically no yolk. Segmentation, as in all telolecithal eggs, is meroblastic since the cleavage planes are only restricted to the germinal disc and do not pass through the whole egg. The segmentation of the germinal disc is very similar to that of other Selachians and closely approximates that of the developing chick. The various later stages of gastrulation with the subsequent origin of the germinal layers is also typical of the class and it is not necessary to elaborate this feature. The folding off of the embryo takes place very early during development, at about 10 days after the egg is laid, the embryo then being about 2 mm. in length and attached to the yolk sac by a very well developed umbilical cord. The vitelline blood vessels at this stage are extremely prominent and spread out over the whole surface of the yolk sac. These vessels or capillaries unite into two median vessels which pass almost completely round the equator of the yolk (Plate IV, Fig. 9) to a region which lies distal from the umbilical cord. Here these vessels break up into two branches running at right angles to the equatorial vessels. These equatorial vessels pass along the sides of the umbilical cord and enter the embryo's heart.

The vitelline circulation is also typically similar to that appearing in the majority of oviparous Elasmobranchs and closely approximates that of the developing chick embryo. The umbilical cord is solid and the vitelline circulation plays a very important rôle in the transference of the nutritive food material from the yolk sac to the developing embryo. The absorption of the yolk material progressively increases with the growth of the embryo, with a concomitant decrease in the size of the yolk sac (cf., Plate IV, Figs. 7, 8 and 9). At an early stage in the development, the external gills, typical of most Selachian embryos, make their appearance

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PLATE IV

Stages in the external development of *H. edwardsii.*

FIGURE 6. The egg case or mermaid's purse, natural size.

FIGURE 7. A mermaid's purse opened to show a developing embryo 25 days old, natural size.

FIGURE 8. A 30-day old embryo. × 1.5.

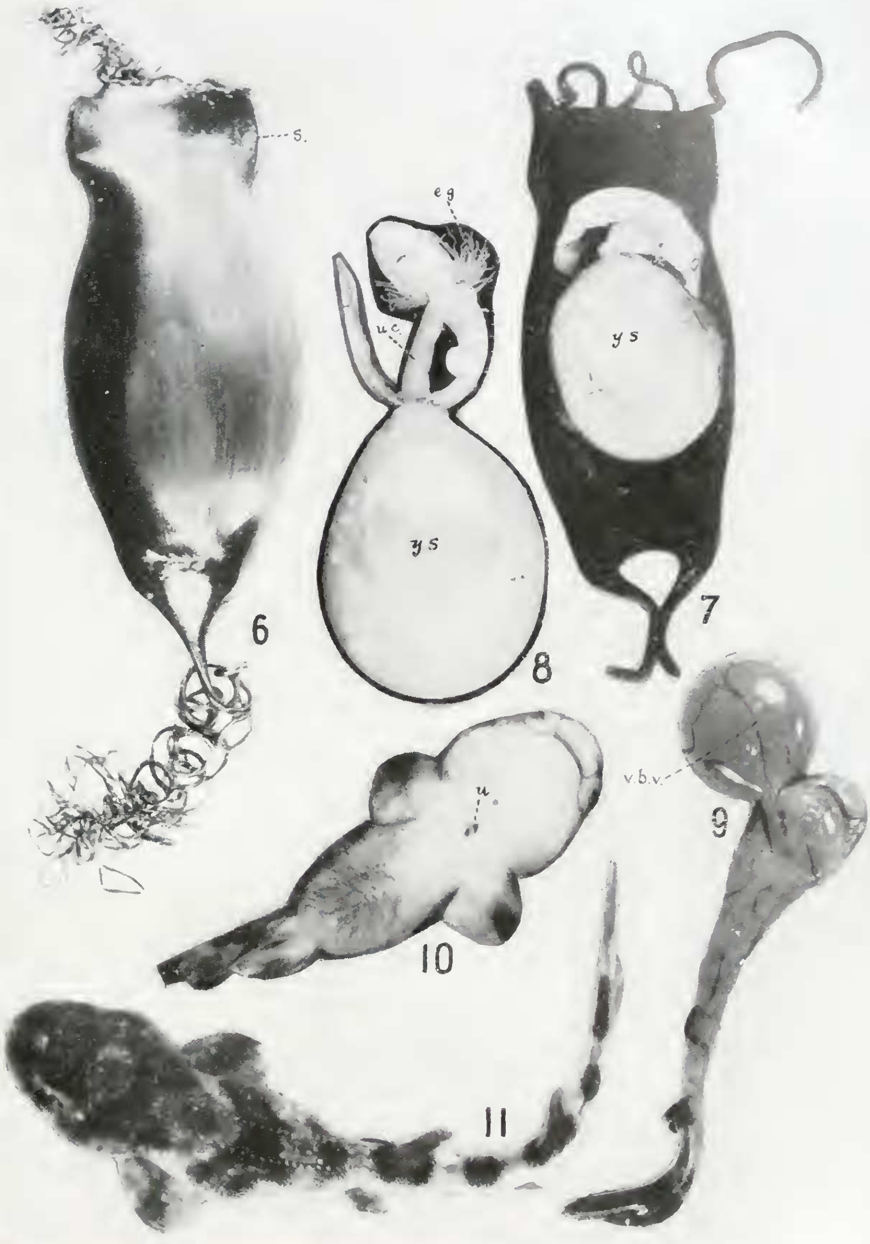
FIGURE 9. A 50-day old embryo. × 1.5.

FIGURE 10. Ventral view of embryo at time of hatching (104 days old). × 1.5.

FIGURE 11. Dorsal view of same.

All Photographs by Author.

Plate IV



(Figs. 7 and 8). In origin these external gill filaments are totally unlike the external gills found in Crossopterygii, Dipnoi, and any Amphibia, and over their function and structure many zoologists have been puzzled.

Graham Kerr (1919, p. 157) states—"While external gills occur within three main sub-divisions of the vertebrates, namely, Teleostomatous fishes (Crossopterygians—the most archaic of existing Teleostomes), Lung-fishes, and Amphibians there are two main groups—Elasmobranchs and Amniotes—in which they are conspicuous by their absence. . . . As it happens, however, there is in the two groups mentioned a definite cause which seems quite competent to account for disappearance of external gills, namely, the development of a new organ—a yolk sac with its highly developed vitelline net work of blood vessels—which in addition to its primitive function must necessarily also function as a very efficient organ of respiratory exchange and so render any pre-existing respiratory organ no longer necessary."

In the present species these external gill filaments are richly supplied with blood vessels and in view of the fact that the embryo studied underwent its complete development in sea water outside of the mermaid's purse it is obvious that their primary function must be a purely respiratory one. The pair of slits in the mermaid's purse previously mentioned must serve for the conveyance of sea water into the interior of the purse where it probably mingles with the layer of albumen surrounding the developing embryo. Although it has been stated that these gill filaments absorb fluids which are milk-like secretions of the uterine mucosa and which serve as food for the growing embryo of all non-placental viviparous sharks and rays (Gudger, 1940) in the present species this is not one of their functions. Beard (1890, p. 310) states—"In the Skate-embryo the filaments are said to disappear shortly before hatching. It may be expected that their atrophy commences when the purse ruptures sufficiently to allow of the passage of sea water directly to the embryo. Then the ordinary piscine mode of respiration would be initiated, and the external gills would disappear." In the present species, however, they have already disappeared during the yolk sac stage when the embryo is 50 days old and the yolk sac has decreased to about half its original size (Plate IV, Fig. 9) and the internal gills are by this time well developed and functional.

At 104 days the embryo has absorbed all the yolk and the yolk sac has shrunk to such an extent that only a vestige of the umbilical cord remains extending through the umbilicus for a length of about 2 mm. (Fig. 10, u.). At the time of hatching the ventral abdominal surface of the embryo between the umbilicus and the cloaca is richly supplied with blood vessels which form a reticulation all over this surface (Fig. 10). The umbilicus persists for about 14 days after hatching and then completely disappears and the fish is fully formed (Fig. 11) and able to fend for itself, swimming about actively. The gestation period of the embryo which developed inside the egg case was also 104 days and the state of development at the time of hatching was the same.

Summary

1. *Haploblepharus edwardsii* is an oviparous dogfish endemic to South African seas.

2. The male and female generative systems are dealt with and specialized features such as the albumen gland, nidamental gland, and the claspers are described.

3. Development takes place in an egg case or mermaid's purse, the gestation period lasting 104 days.

4. The development of an embryo external to the egg case is described.

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